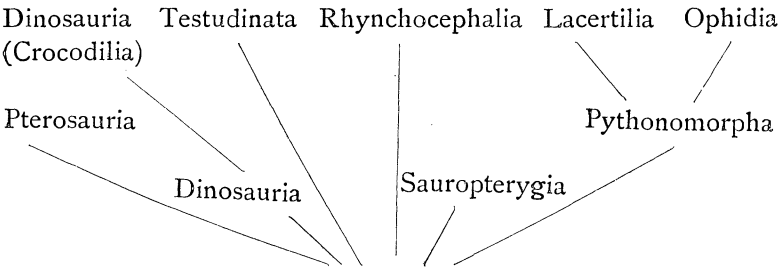
Ichthyopterygia, derived their being from them. The phylogeny may be thus expressed:



(To be continued.)

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ON THE LARVAL FORMS OF SPIRORBIS BOREALIS DAUDIN.

BY J. WALTER FEWKES.

NATURALISTS who are engaged in the identification of the larval forms which marine animals pass through in their growth from the egg, find great difficulty in this study from the lack of direct observations in raising these larvæ from the eggs or in rearing them directly into the adult. This is particularly true in regard to the young of marine annelids, a most profitable field for new observations and one which has had but few cultivators among American naturalists. The following paper is offered as a help to those engaged in this study and not as an extended account of the embryology of the animal of which it treats. It is especially intended for those who are interested in the identification of our marine annelid larvæ.[1]

A genus of chætopod annelids called Spirorbis, as is well known, in its adult and older larval stages, secretes a coiled calcareous case, commonly called its shell, in which it lives. This case is permanently cemented or attached to some foreign body, from which fact the adult is incapable of locomotion. Not so, however, the larva, which is destitute of any such shell, is not fixed but is free swimming, and often captured with the dip-net in surface fishing. From the great dissimilarity in outward form as

[1] The observations here recorded were made in the Zoölogical Laboratory at Newport, R. I. I am indebted to Mr. A. Agassiz for facilities to carry on my studies at that place.

well as the different habitat of the young and adults, the free-swimming larva is often unrecognized or not connected with the genus of which it is the young.

I have often, in former years, captured the larval Spirorbis by surface fishing, but up to a short time ago have been unable to discover to what adult it belongs. Last summer I was fortunate enough to raise these larvæ from the eggs, and am now able to state definitely most of the changes in external form which Spirorbis goes through between the last stages of the segmentation of the egg and the time when it fastens itself to some foreign object and begins its sessile and adult life.

The eggs of *Spirorbis borealis* are easily obtained in considerable numbers. If live adults, enclosed in their cases, be placed in a proper receptacle in water, and the calcareous shells crushed, among the fragments there will be found chains composed of bead-like strings of ova strung along together. These chains are easily distinguished from the other soft parts of the Spirorbis body by their brown or red color. I found a good way to obtain the eggs was to place a number of Spirorbes in a watch crystal with water and then crush the cases with a spatula. Remove the fragments of shells and the strings of eggs are easily seen at the bottom of the watch crystal.

As the adult Spirorbis is very hardy the young can easily be raised from the adult by keeping the latter in an aquarium for a few days, when multitudes of the young make their way out of the worm cases and can be easily found swimming at or near the surface of the water in which they are kept. The young from which the present studies were made were taken in the months of July and August, 1884.

The eggs of *Spirorbis borealis* have a reddish-brown color and are arranged side by side in short strings composed of from one to four rows of from ten to fifteen or more eggs each. The later stages in the segmentation of the egg resemble those of other chætopod eggs and can easily be studied in strings taken from the Spirorbis cases. The younger stages of the segmentation were not found. Each egg is enclosed in a membranous sac, while all the ova lie in a common digitiform structure binding them together. The earliest stages in the development of the larva are passed through while the eggs are thus enclosed.

It will be observed that the larvæ of Spirorbis now to be de-

scribed differ in some particulars from those of "*S. spirillum* Gould (non Pagenst.; an Lam.?)," described by A. Agassiz (*Ann. Lyc. Nat. Hist.*, VIII, pp. 318–323). They differ even more widely from the young of *S. spirillum* described by Pagenstecher (*Zeit. f. Wiss. Zool.*, XII). I regard my larvæ of the same species as that described as *S. spirillum* by Augustus A. Gould (Report on the Invertebrata of Massachusetts [first edition], Boston, 1841).

A. Agassiz says of *S. spirillum* (*op cit.*, p. 318): "The eggs, of a dark reddish-brown color, are found in strings formed of two rows (fig. 18), either on each side of the alimentary canal in the anterior part of the body, where in the adult we find a considerable space free of bristles (as in fig. 25), or else when the strings have been laid they are found on the sides of the body, between it and the limestone tube, and here the young undergo their transformations." Later he says: "The young are quite advanced within the body of the parent previous to the transfer of the egg-sacs to the cavity of the tube where they complete the greater part of their growth." In his figure 18 the larvæ in the strings have already well formed eye spots. I have never been able to observe these larvæ in stages of development in the body of the parent, but have found many specimens of eggs outside the walls of the body of the adult, which were in the last stages of segmentation and therefore much younger than those figured by him (fig. 18).

In the first or youngest stage after segmentation a larval condition was observed in which the embryo almost wholly fills the egg capsule and presents very little differentiation in different regions. This embryo is of an oblong shape and is girt equatorially by a ring of cilia. On one side just below this ciliated belt the wall of the embryo is flattened. The body is opaque, has a dark brown or reddish color, and is destitute of eye spots.

In the next oldest stage (Fig. 1), which is very similar to the young of the genus Pileolaria, figured by Salensky (Etude sur le Developpement des Annelides, Pl. IV, Fig. 7), we have a central, opaque yolk-mass surrounded by a more transparent layer of cells which is thickest on the same side as the flattening noticed in the walls of the larva in a previous stage, a pair of eye spots and a crescentic-shaped body, which is probably lens-shaped when seen in another view, lying between the outer layer of the embryo and its inner cell contents. The external layer I have followed Salensky in regarding as the epiblast and the thin intermediate layer the

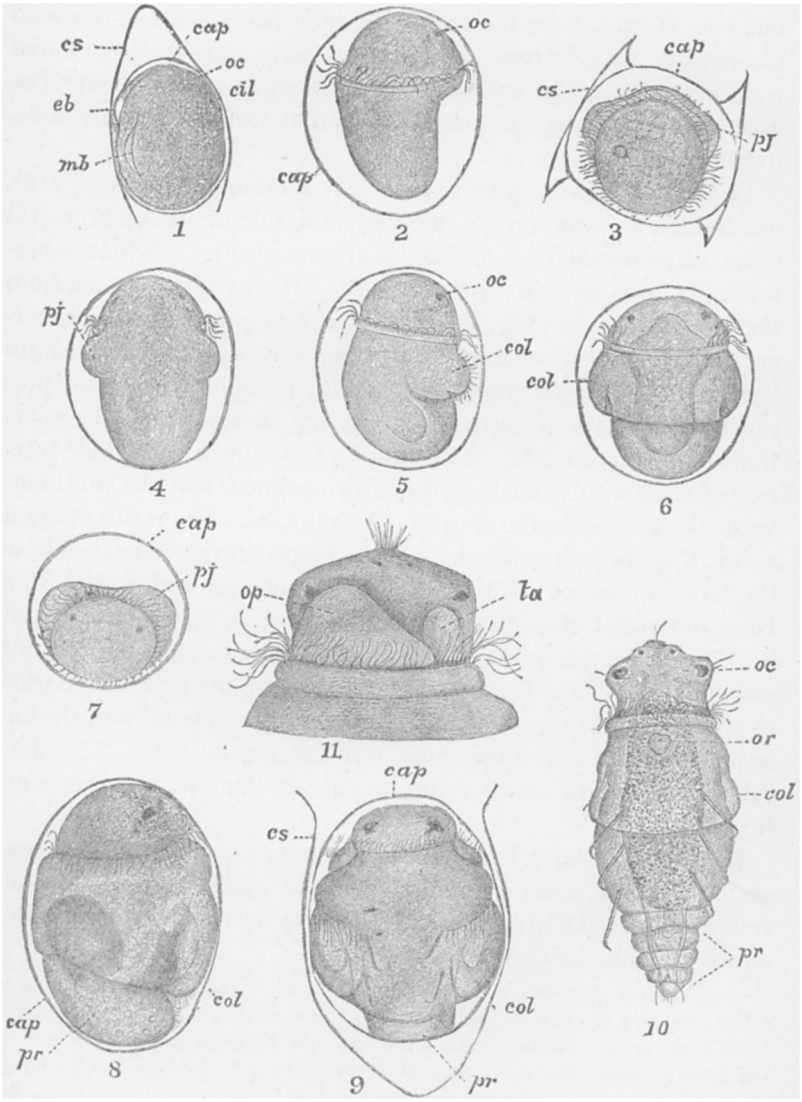
mesoblast. The ring of cilia is seen in profile on each side above the equator of the embryo.

One of the best eggs to use in following the changes has been found to be the last of the chain, since it is always isolated, on one side at least, from the rest. We often find strings of ova with the eggs in a single row. These eggs have always been found well suited for study on account of this simple arrangement. The members of a chain can also be separated from each other without injury.

In the next oldest larva to that just mentioned (Figs. 2, 3, 4), we find the indentation on the flattened side of the embryo still more pronounced than before, as shown in Fig. 2, which represents the larva as seen from one side. If this larva is seen from the posterior pole (Fig. 3), we notice two prominent protuberances which impart to it as seen in this way an irregular triangular shape. From the ventral side (Fig. 4), upon which the protuberances lie, these appendages appear as small lateral projections (*pj*) on each side. The embryo fills almost the whole interior of the capsule in which it is now confined, and the protuberances lie just below the ring of vibratile cilia. From this stage it seems that the collar which is later found on the ventral side of the larva originates as two projections, one on each side. In a larva somewhat older than the last (Figs. 5, 6, 7), the collar (*col*) has formed by the union of the two projections, and has grown somewhat downward over the ventral side of the posterior region of the body. Fig. 7 shows the same embryo as seen from the anterior pole, and Fig. 6 the same from the ventral side. The dorsal surface of the larva is more curved than in younger embryos.

In Fig. 9 the larva is still enclosed in its capsule, and is represented from the ventral region, while the collar is still more developed, and two pairs of single spines were observed in the region partially covered by the collar.[1]

[1] Pagenstecher describes and figures (*op. cit.*, Pl. XXXIX, Fig. 6) a first pair of spines consisting of three on each side at the base of the collar which I have not found in my larvæ. He says, "An der Wurzel des Kragens sprosst das erste Paar von Borstenbündeln hervor, vorläufig mit je drei Borsten." I do not find these represented in the young of *Spirorbis borealis*, and A. Agassiz neither mentions nor figures them in his Spirorbis. My observations do not agree with those of Pagenstecher when he says, "Die erste Spur der Tentacle zeigt sich in Form von drei Höckern jederseits auf dem Kopflappen." I have also been unable to find in my species the oval, green spots, "ovalen gelben Fleck," which he describes "neben dem Magen rechts und links."



Larval forms of *Spirorbis borealis*.

Fig. 9 is the youngest stage of development of Spirorbis in which lateral spines were observed, and in it there are two pairs, a single spine on each side in each pair. This character is also recorded in one of the larval stages observed by A. Agassiz, he says: "The bristles make their appearance in figure 21, where we find two of the three bundles of the collar-like projection of the anterior extremity always distinctly marked in such young embryos." In figs. 4 and 5, Pl. XXXIX, in Pagenstecher's account, it appears in the youngest stage that the spines are represented by a single pair.

The larva in my plate (XI, Fig. 8) is represented as divided into three marked regions, which from now on will be known as the anterior or cephalic, the middle covered on its ventral side by a much larger growth of the collar and a smaller posterior region. The first and second of these divisions are separated by a ring of cilia, the second and posterior by the posterior border of the collar. The prominent lateral ocellus lies on the ventral side of the larva and has a bright red color. The whole body of the embryo is reddish, while the external surface of the collar as well as the ventral region of the posterior part of the embryo is covered with small cilia. On the walls of the ventral region just below the collar there arises a brick-red projection. I have homologized this projection with the "glandes tubipares" described by Salensky in the young of the genus Pileolaria. In this latter genus, however, these glands are arrayed laterally instead of medially and ventrally. In Spirorbis as in Pileolaria I find three ciliated regions which we may follow Salensky in designating: 1. Couronne ciliaire. 2. Couronne ciliaire abdominale. 3. Couronne ciliaire anale.

The interior of the larva on the dorsal side is occupied by a brownish body which is in part the unabsorbed yolk mass.

Through all the stages of growth thus far traced the embryo is still included in its egg capsule. It was observed to fret continually against its envelope and with its spines it constantly presses upon the walls of the same. The motion of these spines shows at once that the egg capsule has flexible walls yielding easily to such pressure. In the next stage (Fig. 10) the larva has become free from the capsule, swimming about in the water with considerable activity. Judging from A. Agassiz's statement in regard to the amount of the development of the side branches of the tentacles,

the young of the Spirorbis which he studied leaves the egg capsule with its cephalic appendages much more developed than I have observed them to be in *S. borealis.* No branching appendages were seen in the youngest larvæ found free in the water in my specimens.

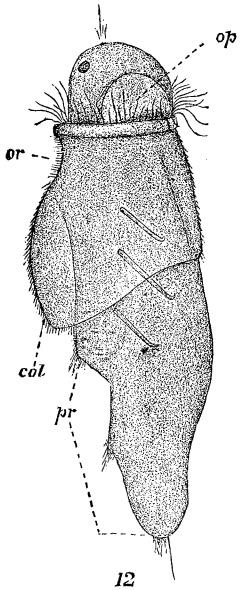
The free larva seen from the ventral side is represented in Fig. 10. It is easily detected in the water on account of its reddish color, although its size is not more than 1^{mm} in length. The larva is more elongated and more vermiform than in previous conditions, and the middle body region is relatively much larger than formerly. It is no longer bounded posteriorly by the posterior edge of the collar.

The head bears four[1] eye spots; two larger, the original ocelli (*oc*), and two small, which are apical, dorsally and medially placed. There is an apical tuft of cilia. The cilia of the belt, between the head and body, are borne on a ferrule-shaped structure which separates the head from the middle body region, and which bears a small ring of cilia on its posterior, a larger on its anterior edge. The mouth opens medially just below this ferrule and above the base of the ventral collar. Its lips are richly ciliated. The ventral collar covers about one-third the middle body region, which is not segmented and bears three pairs of single spines which are falciform at their free extremity. The middle region may be homologized with the anterior body region of such a worm as Prionospio.

The posterior body region is of smaller diameter than the middle and is obscurely segmented. It is ciliated on the ventral side, a prominent ring, "couronne ciliaire abdominale," being formed on the segment nearest the middle division. The posterior extremity of the larva is richly ciliated and bears several short stiff hairs. The whole body cavity, with the exception of that found in the posterior region, has a brick red color. When this larva is seen in profile it will be noticed that the external surface of the collar is ciliated over its whole extent, and that the prominent red projection on the ventral surface of the middle region is also

[1] Pagenstecher says (*op. cit.*, p. 492): "Um diese Zeit bilden sich aus einigen Zellen der äusseren Schicht des vordersten Lappens vier Augenpunkte, von denen die hinteren grösser sind, und auf der Mitte der Stirn wachst eine erst ungemein Classe gerade Borste hervor."

A. Agassiz says: "The ocular spots are always limited to two." The larvæ which I have studied have four and a median flagellum, as described by Pagenstecher.



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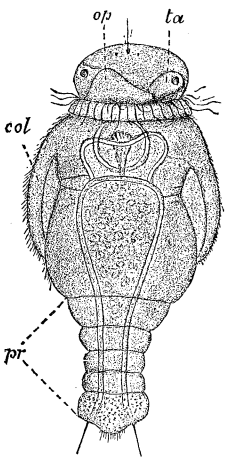

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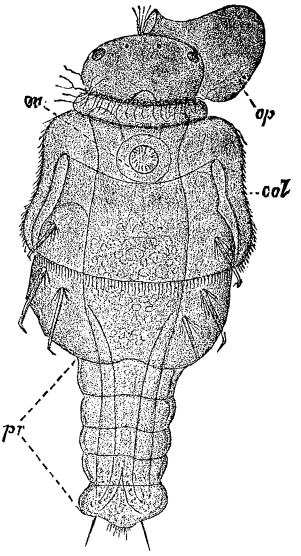

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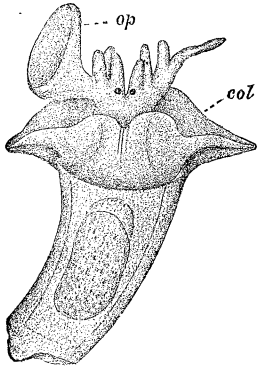

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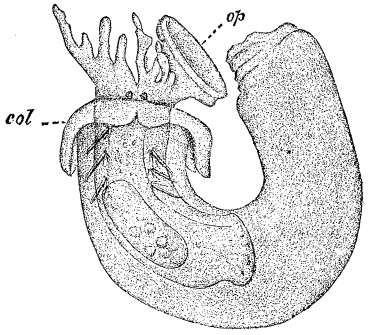

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Larval forms of *Spirorbis borealis*.

covered with cilia. Midway between this last and the posterior extremity of the body is a second prominent tuft, and the very end has a third. Besides these three ciliated regions the whole ventral surface of the posterior part of the body of the larva is clothed with small cilia.

If the cephalic region of the last mentioned larva be looked at from one side (Fig. 12), it will be noticed that on the left hand side of it, snugly approximated to the dorsal walls of the head, there is a thin triangular plate which has begun to push itself up from the region just in advance of the ferrule-like structure upon which the ring of larger cilia is borne. This structure which at first grows out from the left hand side of the neck, and is unpaired is the future operculum.[1] At the time of its origin it is small, and in all stages unpaired, while later in the growth of the worm it assumes a considerable size.

The first appendage to form on the right hand side (Fig. 11) of the larva is a small tentacle, short, stout and club-shaped. I do not find another similar tentacle on the left hand side, but if it exists it may be hidden by the operculum. The better interpretation, however, is, that the operculum where it originates has the form of a simple tentacle with which it is strictly homologous; while the size of the operculum as it grows increases so greatly that it far outmeasures that of the right hand tentacle. My observations do not lead me to think that the tentacles form alternately on the sides of the head of this species of Spirorbis.

Fig. 13 represents a slightly older larva seen from the dorsal side, in which the segmentation of the posterior body region is more sharply defined, and in which also the operculum (*op*) and the right hand tentacle (*ta*) are well developed. In Fig. 14 we have the same larva much older, shown from the ventral side, where the operculum is represented as expanded on the left hand side of the head. In most particulars this larva closely resembles the free larva (Fig. 10).

In a stage which is older than the last the larva has passed into a condition in which not only has the operculum assumed a considerable size, but also several small appendages are found on the head, while of the organs of the head which have disap-

[1] In *S. spirillum*, according to A. Agassiz, "the first tentacle appears on the right, next comes the corresponding tentacle of the left, and only later the rudiment of the odd opercular tentacle covering in figure 21 the right tentacle." The operculum was the first cephalic appendage which was observed in the larvæ which I studied.

peared, the most important is a pair of the ocelli, the first to originate and for a long time the most prominent eye spots found on the ventral cephalic prominences. The apical ciliated tuft of former stages has also disappeared. The apical eye spots still remain.

Of the appendages to the head we notice on the right hand side instead of the club-shaped tentacle which formerly existed there, that the place is now occupied by an elongated body with beginnings of side branches, a structure which later forms a branchia. On the left hand side, near the operculum, are small projections which later develop into the left hand branchia, while medially appear two prominences, one upon the other. In the development of the larva of Spirorbis it looks as if we had, as I have already shown,[1] in a larva which is provisionally identified as the immature Prionospio, and as Salensky has found in Pileolaria, temporary cephalic tentacles which later give place to the permanent branchiæ of the head. In the right hand branchia, now of considerable size, we formerly had a small tentacle which, although it never reaches the great size of the temporary tentacle of Prionospio, is so closely similar both in size and general appearance to the temporary tentacle of Pileolaria, as described by Salensky, that it is in Spirorbis placed in the same category.[2]

The passage of the free larva of Spirorbis into the form with a case is a most interesting process, and one which is by no means simply in the changes involved. It can easily be observed in early conditions and the interior even of the larva studied, since the external case, when first formed, is almost wholly transparent.

At this age the larva becomes attached to the walls of the vessel in which it is confined preparatory to the secretion of a shell. In many specimens, however, the following condition, which although probably abnormal, was most advantageous to a study of the secretion of the tube, was observed. The free larva often

[1] Bull. Mus. Comp. Zoöl., Vol. XI, No. 9.

[2] I do not consider that the worm represented in fig. 57 of A. Agassiz's paper (*op. cit.*) is, when compared with fig. 56, an instance of retrograde development. Fig. 57 bears a strong likeness to *Alaurina prolifera* commonly looked upon not as an annelid but as a turbellarian. If the worm is an Alaurina I cannot regard the larva represented in fig. 56 as its young. The adult of fig. 56 is unknown, and it is extremely doubtful that it ever loses its cephalic spines and appendages and passes into fig. 57. It may or may not resemble Prionospio in a subsequent modification of the cephalic tentacles into branchiæ.

does not immediately settle to the bottom prior to the secretion of the case in which it lives, but passes through preliminary stages while floating on the water. Upon the surface of my aquaria, with its Spirorbis, I found a multitude of small white bodies, unattached, which on close examination were found to be Spirorbis larvæ in which the shell had just begun to be secreted. They float on the surface for a short time until the increasing specific gravity of their bodies sinks them to their future homes.

Fig. 15 represents an example of a larva of this kind in which the head and collar is half protruded outside of the cavity of the case in which the larva is found. The head and branchial appendages occupy the middle of the figure at the top, while the expanded trumpet-shaped structure below it is the half protruded collar. It is extremely difficult to draw accurately the outlines of a specimen of Spirorbis in this stage when wholly or partially expanded and alive, from the fact that the movements are so quick in retracting itself into the case, and the animal is so sensitive to any small motion in the immediate vicinity. It has been almost impossible for me to observe the expanded Spirorbis long enough to draw anything more than a simple outline with the camera. This difficulty increased with the growth in age of Spirorbis.

The case or shell of the larva, Fig. 15, is not at first coiled, but slightly curved, horn-shaped, well formed at its larger end, with less solid walls at the smaller extremity. The most prominent structure in the body of the larva is an oblong mass of cells of brick red color seen through the transparent walls of the shell. In the next stage (Fig. 16) which was also found floating on the surface of the water, the shell has elongated and become partially coiled, but is still transparent and in places more or less flexible in character. The larva now occupies not more than one-half of the whole length of the case when the appendages to the head are expanded. Fig. 16 represents this larva taken on the surface of the water prior to attaching itself to some foreign object. The branchial appendages to the head are more completely developed in this than in previous conditions in the growth of Spirorbis. The ciliation upon them is also more conspicuous than in previous embryos. The operculum is represented on the right hand side of the figure.

The collar, which when the head is extended from the case, is reflexed over the edge of the shell, is clothed with minute cilia. As in previous larvæ, drawings are very difficult to make on account of the quick motion in the retraction of the head, in this the difficulties are even greater. A camera drawing of the case is, however, very easy to obtain from its more solid nature. The soft parts were taken from a specimen which was dead, but not distorted by the conservative fluids in which it was preserved,

On the body of the worm three pairs of spines, which are hook-shaped at their extremities and connected with the body walls by strong muscles, were observed. These spines are placed as in early stages upon the anterior body region, and are very prominent. The posterior body region is destitute of spines in this stage. One of the most conspicuous structures in the body of the worm is a large oblong mass, of reddish color, easily seen through the transparent walls of the case which encloses the worm. The size of the worm is 2^{mm} measured from one side of the coiled case to the opposite side.

EXPLANATION OF THE FIGURES.

cap, capsule in which the embryo is enclosed.
cs, covering in which the "strings" of ova are found.
cil, cilia.
col, collar.
eb, epiblast.
mb, mesoblast.
oc, ocellus.
op, operculum.
or, mouth.
pj, projections which later grow together and form the collar.
pr, posterior body region.
ta, tentacle.

PLATE XI.

FIG. 1.—The terminal egg of a string in its capsule after segmentation and formation of layers and cilia. Larva in capsule and chain.

(Figs. 2–4, the same embryo still in capsule older than the last.)

" 2.—Lateral view.
" 3.—From posterior pole. Larva in capsule and chain.
" 4.—From ventral side.

(Figs. 5–7, still older larva.)

" 5.—Lateral view.
" 6.—Ventral view.
" 7.—View from anterior pole.
" 8.—Lateral view of a larva slightly more mature than the last.
" 9.—Older larva from ventral surface just before escape from its capsule. Terminal larva in the chain.

FIG. 10.—Free young captured on surface of the water in glass jar containing specimens of the adult. Size 1^{mm}.

" 11.—View of the head of a young Spirorbis older than the last with the beginning of the operculum and the right hand tentacle, seen from the dorsal side.

PLATE XII.

FIG. 12.—Side view of a larva of the same age.

" 13.—The same larva older, seen from the dorsal side.

" 14.—An older larva seen from the ventral side.

" 15.—Larval Spirorbis which has just begun to secrete its shell, shown with the collar and head partly protruded.

" 16.—An older larva with shell more completely formed than in the last. The head and collar are extruded. Size 2^{mm}.

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PENNSYLVANIA BEFORE AND AFTER THE ELEVATION OF THE APPALACHIAN MOUNTAINS, A STUDY IN DYNAMICAL GEOLOGY.

BY PROFESSOR E. W. CLAYPOLE.

THE geologist traveling or working among the contorted strata of Pennsylvania can scarcely escape being struck by the immense compression which the rocks of that part of the country experienced during the folding process which was the first stage in the formation of its mountain ranges. By this term I do not mean merely the condensation of the rock-masses by the tangential pressure to which the folds are due, but the actual shortening of the surface which must have resulted from the folding.

Doubtless the thought has occurred to others, but I do not recollect seeing it put forward or developed to its legitimate conclusions. Yet it is obvious that so extensive a corrugation of the earth's crust manifesting itself by the production of several wide anticlinal arches, from which the present mountains have been carved, must have been accompanied by a diminution of the area over which those strata previously extended.

To measure as nearly as practicable the extent of this contraction of the surface and to set forth the more important conclusions deducible therefrom are the objects of this paper.[1]

To prevent undue extension in treating the subject, it will be necessary to assume certain propositions. These will be here

[1] An abstract of this paper was read before the British Association at Montreal in August, 1884.